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RESEARCH ARTICLE

Habitat filtering and inferred dispersal ability condition across-scale species turnover and rarity in Macaronesian island spider assemblages

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Abstract

Aim: Habitat diversity has been linked to the diversity and structure of island communities, however, little is known about patterns and processes within habitats. Here we aim to determine the contributions of habitat type and inferred dispersal frequency to the differences in taxonomic structure between assemblages in the same island habitat.

Location: The Macaronesian archipelagos (Azores, Madeira, the Canary Islands and Cabo Verde).

Taxon: Spiders (Araneae).

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Methods: We established forest and dry habitat sites (each with five plots) on two islands per archipelago. We collected spiders using standardised sampling protocols. We tested the differences in beta diversity separately for each habitat and for each inferred category of ballooning (an aerial dispersal strategy) frequency across geographic scales through nested non-parametric permutational multivariate analyses of variance. We then tested whether ballooning and habitat influenced heterogeneity in species composition (dispersion in beta diversity) in the two habitat types. We analysed the effects of habitat and ballooning on species abundance distribution (SAD) and rarity by fitting Gambin models and evaluating the contribution of ballooning categories to SAD.

Results: Communities of the same archipelago and habitat were taxonomically more similar, and beta diversity increased with geographic scale, being greater in dry habitats. There was greater species replacement among assemblages in dry habitats than in forests, with greater differences for rare ballooners. There were no differences in SAD between habitats although dry habitat sites seemed to harbour more species with low abundances (rare species) than forests.

Main conclusions: Habitat type does not only condition the differences between spider assemblages of the same habitat but also the scale at which they occur. These differences may be determined by the heterogeneity in the physical structure of each habitat as well as how much this structure facilitates aerial dispersal (ballooning), and should be considered in theories/hypotheses on island community assembly as well as in conservation strategies.

KEYWORDS
Araneae, beta diversity, COBRA sampling protocols, neutral processes, niche processes, rarity

1 | INTRODUCTION

While habitat (and its microhabitats) may filter the species that can survive and/or establish at a given site, the origin and rate at which specimens or propagules of such species reach those sites will be determined by their dispersal ability (Cornell & Harrison, 2014; Leibold et al., 2004; Zobel, 2016). Even under stochastic processes (Hubbell, 2001), the ability of a species to disperse may be constrained by its relative body size, the environmental conditions that it can endure and the geographic scale at which it moves (Morlon et al., 2008). Indeed, when it comes to the source species pool, the origin of moving individuals is biased towards nearby areas with similar environmental and habitat conditions (Cornell & Lawton, 1992; Cuellar-Gempeler & Leibold, 2019). These factors become stronger, and the resulting patterns in community composition and structure become more marked when the target locations are remote and/or surrounded by unsuitable habitats (Mohd et al., 2018), such as in the case of islands. On islands, dispersal ability establishes a powerful filter for community assembly (Carstensen et al., 2013; Wang et al., 2018), reflected in species richness, rarity, coexistence and structure (Chase, 2003; MacArhur & Wilson, 1967; Tilman, 1994).

Islands have long been considered natural laboratories and appropriate model systems to understand ecological and evolutionary processes, and the role played by habitats in community assembly (Kirkby et al., 1968; Steinbauer et al., 2016; Whittaker & Fernández-Palacios, 2007; Whittaker et al., 2008). Although the diversity of habitats has been linked to the diversity and structure of island communities at the regional or island scales (Whittaker et al., 2008), little is known about the patterns and processes at the local or within-habitat scale (Cardoso, Gaspar, et al., 2010; Marsh et al., 2010). Indeed, this lack of knowledge is not exclusive of habitats on islands and there is still a limited amount of within-habitat comparative research (Burnham, 2004; Newbold et al., 2016; Role et al., 2020; Soininen et al., 2007; Wang et al., 2013), partly because of the assumption of within-habitat community homogeneity and dispersal-dominated processes (Harborne et al., 2006).

Environmental variability (Busse et al., 2018) or tolerance (Chase, 2007), and disturbances (Hawkins et al., 2015) may be behind within-habitat differences between communities in terms of species composition and species abundance distribution (SAD; Matthews & Whittaker, 2014; Tsafack et al., 2021). The deficit of humidity, for instance, may increase dissimilarity between communities throughout time within habitats (Tsafack et al., 2019). This pattern may be the result of smaller fluctuations (greater stability) in the levels of humidity (usually correlated with temperature) in forests than in open

habitats, due to the protective effect of the canopy (Lin et al., 2020). However, beta diversity (as a measure of community dissimilarity) has also been found to be greater between localities within forests than between localities within grasslands (Picone, 2000; Stanton, 1979). Therefore, the relationship between habitat type and community dissimilarity remains unclear, partly because forest versus grassland comparisons are extremely scarce, they come mainly from local scale studies or distant plots (Gregorič & Kuntner, 2009) and there have been practically no attempts to test them at the regional scale.

Spiders are one of the most ubiquitous and diverse taxa in terrestrial ecosystems (Coddington & Levi, 1991). These arthropods are useful for understanding how dispersal and habitat interact (Florencio et al., 2016; Gavish & Ziv, 2016; Malumbres-Olarte et al., 2014), and in the field of insular biogeography, they are providing evidence of how isolation, mobility and microhabitat size affect the functionality of species and assemblages (Méndez-Castro et al., 2020) as well as colonisation and vicariance processes across archipelagos (Čandek et al., 2019; Gillespie, 2002; Rominger et al., 2015). Furthermore, spiders can be used to understand the effects of dispersal, between-habitat differences and disturbance on the SADs of assemblages, providing useful information for conservation management (Boieiro et al., 2018; Borges et al., 2008; Cattin et al., 2003; Kaltsas et al., 2019; Kondratyeva et al., 2019; Leroy et al., 2014; Morel et al., 2019). However, when it comes to within-habitat patterns, very little is still known.

Spider dispersal is notably characterised and determined by ballooning: the strategy of releasing threads of silk that are used as parachutes or 'balloons', through which individuals are capable of long-distance dispersal (Bell et al., 2005; Reynolds et al., 2007). Tendency to balloon varies across species and families, so frequent ballooners may disperse more and have larger distributions (Carvalho & Cardoso, 2014; Malumbres-Olarte, Crespo, et al., 2020). Although this variability has been found to have effects on assemblage dissimilarities (Carvalho & Cardoso, 2014; Wu et al., 2017), it remains untested if and how the effects of dispersal ability on spider assemblages change according to habitat type, particularly those on islands.

The oceanic archipelagos of Macaronesia have become a paradigmatic model system in community assembly and island biogeography (Cardoso, Arnedo, et al., 2010; Steinbauer et al., 2013) and are included in the Mediterranean biodiversity hotspot (Myers et al., 2000). Because of their climatic heterogeneity, these archipelagos present a range of habitats, from extreme arid regions to lush forests (Fernández-Palacios et al., 2017; Juan et al., 2000), and can therefore serve as models to study the interactions between dispersal and the filter applied by different habitats on communities (Fernández-Palacios, 2010).

Our aim here was to determine the contributions of habitat type and inferred dispersal ability (ballooning) to the variation in the taxonomic structure of spider assemblages and to quantify this variation across spatial scales. Our two target habitats are the native forests and the dry open scrubland-grasslands habitats. After exploring the general spatial patterns in the composition of spider assemblages, we tested three hypotheses: (H1) the increase in the differences between assemblages (represented by beta diversity) with geographic scale caused by the increase in isolation should be greater for dry habitat assemblages than for forest assemblages because in the former the (micro)climatic conditions are less stable (acting as an environmental filter) and the habitat more heterogeneous in space; (H2) the differences between assemblages found in the same habitat should be driven by spiders with poor ballooning (dispersal) ability, whose species turnover may be greater—in the two habitats but particularly in dry habitats because of its less stable (micro)climatic conditions and its greater spatial heterogeneity (H1); and (H3) resembling the effects of disturbances, a greater (micro) climatic instability may lead to greater species rarity, resulting in SADs that follow a log series in dry habitats (as in disturbed areas) and a log-normal in forests (as in undisturbed areas). These differences may be more pronounced among poor dispersers, whose recolonisation ability is limited and populations may fluctuate more spatio-temporally.

2 | MATERIALS AND METHODS

2.1 | Spider sampling and data generation

Our model system was the Macaronesia, an oceanic region composed of five archipelagos: the Azores, Madeira, the Canary Islands, Cabo Verde and Selvagens. We applied a partially nested sampling design with 60 plots of 50 × 50 m set up across the first four aforementioned archipelagos (Figure 1; Table S1 in Appendix S1). Within each archipelago we selected two islands and, on each island, we set up one or two groups of plots termed hereafter *sites*—with the exception of Madeira island, where we set up three sites (two forest sites and one dry site). Each site was composed of five plots (P1–P5), placed at increasing distances from a first reference plot: P1 at point 0, P2 at 0.1 km from P1, P3 at 1 km from P1, P4 at 5 km from P1 and P5 at 10 km from P1. Therefore, our design consisted of plots within sites, sites within islands and islands within archipelagos. We considered that, although not completely balanced, this design was the best possible one to achieve our objectives (including testing the difference between forest and dry habitat assemblages across Macaronesian archipelagos) given the conditions of the habitats and islands—the location and availability of the appropriate areas for sampling (they had to be logistically accessible and at the wanted distances), the extent of the habitats on each island (some habitat was present only in certain islands or areas) and the size of the islands (most islands could not fit more than one site [5 plots]).

Half of the 60 plots were in mesic native forests and the other half in native open dry habitats, with each site containing only plots of one habitat type. Depending on the availability of habitat types, we established sites of both forest and dry habitat plots on the same island (as in the case of La Gomera and Tenerife in the Canary Islands, and Madeira Island), or only sites of forest plots (the Azorean islands of Pico and Terceira) or only dry habitat plots (the Madeiran

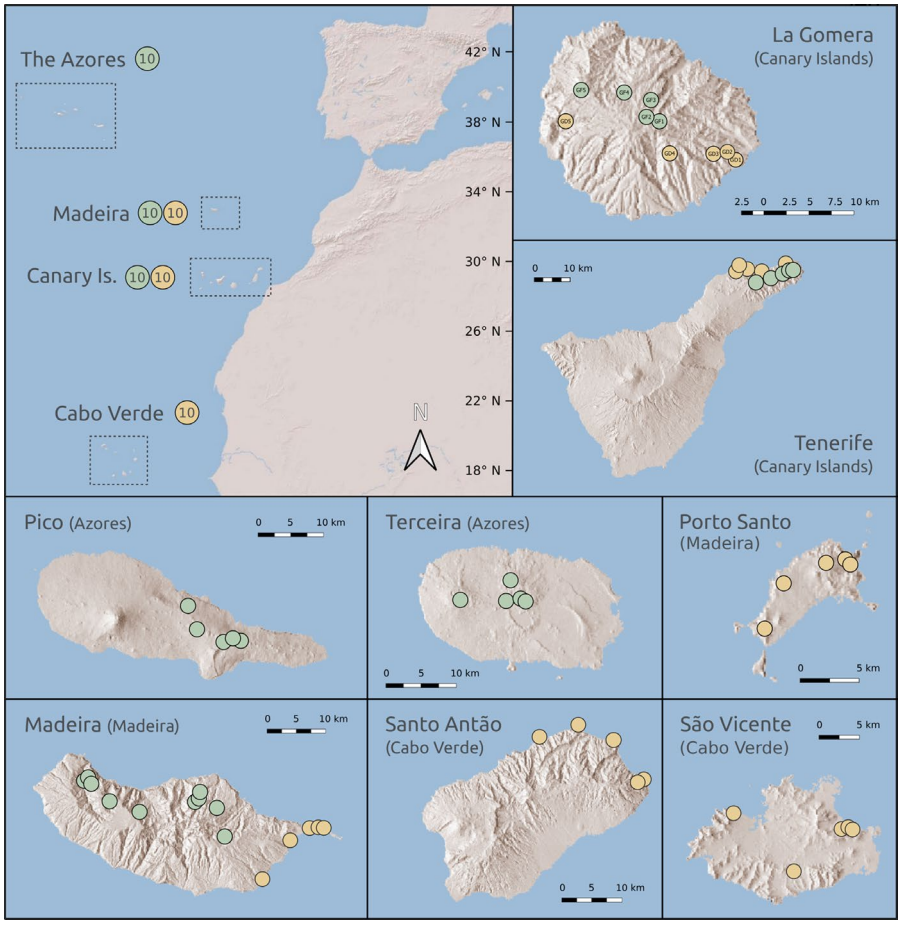

FIGURE 1 Macaronesian biogeographic region (Selvagens islands are not marked) with the number of dry habitat (ochre circles) and forest (green circles) plots per archipelago, and the eight sampled islands with the locations of their corresponding plots. La Gomera island (Canary Islands) serves as an example of the sampling design, with dry habitat (GD1-5) and forest (GF1-5) plots placed at increasing distances. Islands are not at the same scale

island of Porto Santo, and the Cabo Verde islands of São Vicente and Santo Antão). Therefore, five islands contained forest plots (Pico and Terceira in the Azores, Madeira island, La Gomera and Tenerife in the Canary Islands) and six contained dry habitat plots (Madeira island and Porto Santo in Madeira, La Gomera and Tenerife in the Canary Islands, São Vicente and Santo Antão in Cabo Verde).

In each of the plots, we collected spider specimens using the COBRA sampling protocol, a standardised and optimised protocol that combines different sampling methods to obtain the maximum possible number of species for a given amount of effort and produces comparable data (Cardoso, 2009; Malumbres-Olarte et al., 2017). The sampling methods of the COBRA protocol for dry habitat were pitfall trapping (12 samples, each one grouping four individual pitfall traps), nocturnal and diurnal sweeping (four samples each), and nocturnal active ground search (four samples). In forest plots, the COBRA protocol consisted of pitfall trapping (12 samples, as in the dry plots), diurnal and nocturnal sweeping (two plus two samples), diurnal and nocturnal foliage beating (two plus two samples) and nocturnal aerial active search (four samples). Therefore, we obtained a total of 24 samples per plot in both dry and forest habitats. In La Gomera and Tenerife dry habitats the great abundance of shrubs allowed the split of the four sweeping samples in two sweeping and two beating samples. Sampling occurred between 2012–2017—Terceira forest (2012), Tenerife forest (2013), Pico forest (2016), Madeira forest (2016), La Gomera forest (2016), and all dry plots in Madeira, Canaries and Cabo Verde in 2017, always at the time of the year with the greatest levels of diversity (April–November).

We identified all adult spider specimens to species or, whenever the specimen was recognised as a non-described species, to morphospecies (Azorean and Madeiran data are available on Malumbres-Olarte, Boieiro, et al., 2020; Malumbres-Olarte et al., 2019, and data from the Canary Islands and Cabo Verde are in preparation). In cases where morphological characters were not sufficient for a reliable identification—especially when dealing with sister species, we used DNA sequences (mitochondrial cytochrome c oxidase 1 gene and the slowly evolving nuclear 28s rRNA gene) to discriminate them (details on the molecular methodology and the obtained sequences are included in Appendix S2, but see also Emerson et al., 2017 for a similar approach).

Once all (morpho)species were identified, we classified them according to a ballooning frequency—frequent, occasional and rare (infrequent or no ballooning) ballooners—using current knowledge on each of the families to which we assigned the (morpho)species, and when possible, on species-specific information (especially in the case of Azorean species, which are better known). Ballooning consists of the aerial non-directional movement of small invertebrates by using silk threads to catch air currents and is the main long-distance dispersal strategy used by spiders. Ballooning frequency may vary due to endosymbiotic infections (Goodacre et al., 2009) or selection pressures (Gillespie et al., 2012). Insular species, for instance, tend to evolve towards reduced ballooning propensity, as ballooning may

be disadvantageous when surrounded by a large inhospitable matrix (Gillespie et al., 2012). Nevertheless, even in these cases, the current ballooning propensity of the descendants of frequent ballooners should be greater than that of the descendants of rare ballooners; and these differences should be reflected in the current compositional patterns of assemblages. We acknowledge that this assumption is debatable; however, because of the scarcity of species-level information (it is virtually impossible to obtain species data on ballooning propensity for such a large number of species, some of which are still unknown to science), we consider family-level classification (and therefore, inference) to be an appropriate surrogate of general ballooning propensity, and therefore, of potential dispersal or colonisation ability (Carvalho & Cardoso, 2014; Macías-Hernández et al., 2020). Furthermore, we believe that our coarse-scale and ordinal classification of species according to three ballooning frequency categories reduces the chances of dispersal propensity miss-classification.

All Azorean, Madeiran and Cabo Verde voucher specimens were deposited at the EDTP—Entomoteca Dalberto Teixeira Pombo, University of Azores, Campus of Angra do Heroísmo, Portugal, and the specimens from the Canary Islands at the invertebrate collection of the Instituto de Productos Naturales y Agrobiología (IPNA-CSIC), Tenerife, Spain.

2.2 | Statistical analyses

2.2.1 | Beta diversity and dispersal-related composition

As a first general assessment of the diversity and sampling thoroughness of the 60 studied assemblages, we evaluated the completeness for each site using the coverage estimator ($\hat{C}_n$, Chao & Jost, 2012), which estimates the proportion of the total number of individuals of an assemblage that belongs to the species represented in the sample, and the Chao1 (P-corrected) non-parametric estimator . We then visualised the general differences between assemblages across archipelagos through non-metric multidimensional scaling (NMDS; McCune & Grace, 2002) using the incidence-based Jaccard index (Jaccard, 1912). We investigated the relative positional contribution of inferred dispersal abilities to the clustering of assemblages (plots) by plotting species in the same ordination space and depicting them according to their ballooning category (frequent, occasional or rare ballooners) and their abundance across all assemblages. We calculated the proportion of species of each ballooning category in each plot and tested if there were differences between habitats using nested linear models, with sites nested in archipelagos and archipelagos nested in habitats as the model structure.

2.2.2 | Community variation across geographic scales

To test whether and how the differences between assemblages increase with geographic scale (H1) we partitioned beta diversity using the Jaccard index so that $\beta_{total} = \beta_{replacement} + \beta_{richness}$ (Carvalho et al., 2012). We favoured this beta partitioning approach described and recommended by Carvalho et al. (2013) and Schmera et al. (2020) because we consider it the most suitable to answer our questions. We acknowledge the fact that the approach by Baselga (2010) may be the most commonly used amidst the ongoing debate (Schmera et al., 2020). However, in the present study, we are interested in the replacement of species (the species substituted when comparing two assemblages) and the differences in richness (the loss/gain of species), which, in our view, are the basic processes behind beta diversity and, conceptually and mathematically, only the framework by Carvalho et al. is able to properly quantify (see also Legendre, 2014).

We investigated how β_{total}, $\beta_{replacement}$ and $\beta_{richness}$ varied depending on three variables—spatial scale (between archipelagos, within archipelagos or within sites), habitat (forest or dry) and species with different inferred dispersal abilities (frequent, occasional or rare ballooners)—by partitioning β diversity for each combination of the three variables. Subsequently, we conducted nested non-parametric permutational multivariate analyses of variance (PerMANOVA) to test for differences in β_{total}, $\beta_{replacement}$ and $\beta_{richness}$ between archipelagos and between sites within archipelago, for all species and for each ballooning group of species separately for both forest and dry habitat, using permutation tests with 9999 iterations (Anderson, 2001). When a factor showed a $p < 0.05$, we used pairwise PerMANOVA tests to identify pairwise differences between the levels of the factor(s) that showed $p < 0.05$.

2.2.3 | Community variation within habitats

For our second hypotheses (H2), we tested whether the differences between assemblages of the same site (within-site beta diversity) were influenced by the habitat and the inferred ballooning frequency of species. We implemented a permutational analysis of multivariate dispersions (PERMDISP; Anderson et al., 2006) to calculate the average distance of sampling units (i.e. plots) to their group (i.e. sites) centroid in the euclidean space defined by a principal coordinate analysis. We applied this analysis specifically to β replacement (i.e. the measure of the process of species replacement behind community/assembly turnover) for all species and for each ballooning group. We then used the distances obtained from the PERMDISP in linear mixed models to test for differences between habitats using archipelagos and sites nested within archipelagos as random effects.

2.2.4 | Species rarity

For our third hypothesis (H3) we examined the variation in species relative abundances and rarity patterns across sites by inspecting the SADs using the gambin model (Matthews et al., 2014; Ugland et al., 2007). The unimodal gambin model has a single free parameter (α), which characterises the distribution shape with low values indicating logseries-distribution and higher values indicating more

lognormal-distribution. Gambin has been shown to provide good fits to a wide variety of empirical datasets (Matthews et al., 2014). Given that SAD model parameters are sensitive to variations in sample size (Magurran & McGill, 2011) and that we were also interested in comparing parameter values across sites and habitats, we used a procedure where, for each site, we subsampled 400 individuals (the least abundant sample having 483 individuals for the dry site in São Vicente, Cabo Verde), fitted the best gambin model to this subsample and stored the α parameter value(s). Given that this subsampling procedure is stochastic, we repeated the process 100 times for each sample and took the mean α value. We tested whether habitat type had an effect on the α parameter using a Wilcoxon test. Finally, we tested whether mean weighted octaves (i.e. weighted by species number) differed between ballooning categories in dry and forest sites separately—rare species are associated with low mean weighted octaves and abundant species with high mean weighted octaves—with Kruskal–Wallis followed by post-hoc Dunn tests.

We handled and analysed all our data with R 3.6.1 (R Development Core Team, 2020) using multiple packages including VEGAN (Oksanen et al., 2020) and BAT (Cardoso et al., 2015).

3 | RESULTS

3.1 | Beta diversity and dispersal-related assemblage composition

We collected a total of 15,686 spider specimens, which we identified to 360 species or morphospecies belonging to 37 families. The number of observed species per plot ranged from 9 (plot 4 of São Vicente, Cabo Verde) to 57 (plot 1 of dry habitat on La Gomera, the Canary Islands). Sampling completeness values ranged between 0.89–0.99 (median = 0.97) and between 0.37–0.99 (median = 0.76), for coverage and Chao1-based measures respectively (Table S1 in Appendix S1).

The incidence-based NMDS ordination showed that spider assemblages across Macaronesia grouped according to the sites and archipelagos to which they belonged (Figure 2a). Also, forest and dry habitat assemblages grouped separately and distinctively along the first axis of the ordination. In the NMDS based on ballooning frequency and species abundance, plots also grouped according to the archipelago that they inhabit. According to this ordination, there were more rare ballooners among the species with the highest abundance (four islands; Figure 2b).

Proportions of species belonging to the three ballooning categories showed similar patterns across all four archipelagos, with more frequent ballooners and fewer rare ballooners in forest plots than in dry habitat plots (Figure 2c). Nested linear models confirmed the observed patterns in the three ballooning categories—the number of spiders belonging to each category varied depending on habitat and archipelago (but also site; Table 1). Habitat was the variable with the largest effects on the number of frequent and rare ballooners (with R^2 values of 57% and 63% respectively) although archipelago also had a substantial effect (R^2 = 26% and 23%). Occasional ballooners

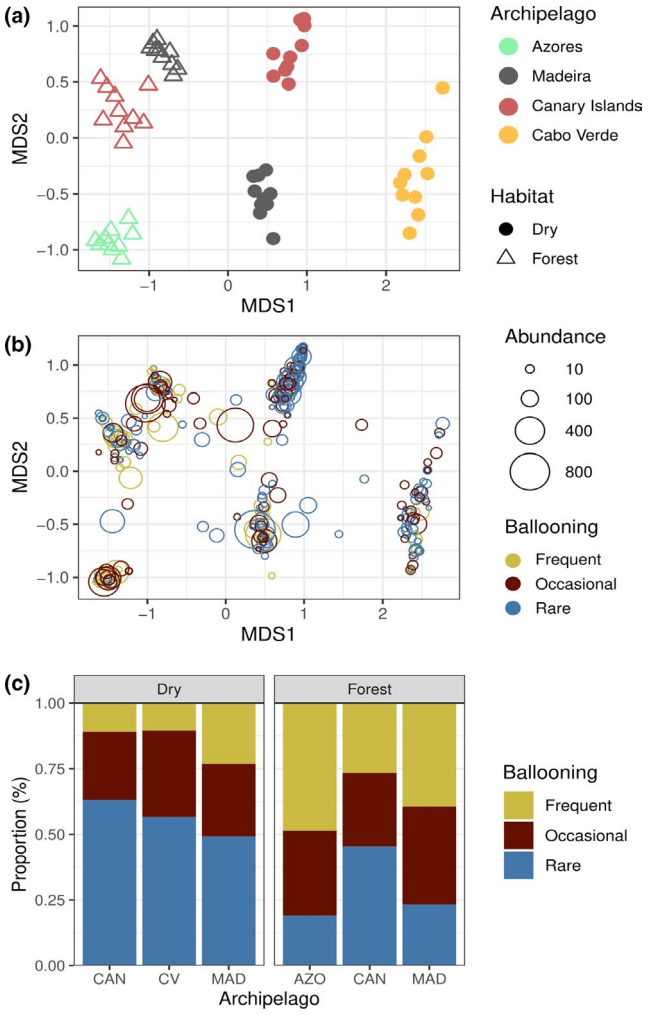

FIGURE 2 Composition according to habitat type and ballooning frequency of the spider assemblages of the Macaronesian archipelagos. (a) Non-metric multidimensional scaling ordination based on species incidence (Jaccard index), with each circle representing a community (plot). (b) Non-metric multidimensional scaling ordination based on the species incidence (Jaccard index), with each circle representing a species, with circles (species) classified according to ballooning frequency and size proportional to their mean abundance. (c) Proportion of species of each ballooning category in each archipelago

were affected by all hierarchical levels but showed lower R^2 than the other two ballooning categories.

3.2 | Community variation across geographic scales

Overall, the greater the geographic scale, the greater the observed β diversity (Figure 3) and, for most species groups and scales, $\beta_{replacement}$ was always greater than $\beta_{richness}$. However, the patterns varied depending on ballooning category and habitat type. Occasional and frequent ballooners showed decreasing values of $\beta_{replacement}$ as the spatial scale increased, whereas rare ballooners kept high values across spatial scales in a dry habitat. Interestingly, $\beta_{richness}$ was higher

TABLE 1 Results of the nested linear models testing the effects of habitat, archipelago (within habitat type) and site (within archipelago and habitat) on the proportion of species belonging to different ballooning categories. We provide degrees of freedom (df), the *F*-ratio (*F*), its associated *p*-values (*p*) and the of Nagelkerke's R^2 for each effect

Ballooning category	Effects	df	*F*	*p*	R^2
Frequent ballooners	H	1	193.54	<0.001	0.57
	H/A	4	21.95	<0.001	0.26
	H/A/S	6	1.82	0.115	0.03
	R	48			0.14
Occasional ballooners	H	1	5.69	0.021	0.06
	H/A	4	4.08	0.006	0.17
	H/A/S	6	4.30	0.002	0.27
	R	48			0.50
Rare ballooners	H	1	304.42	<0.001	0.63
	H/A	4	28.12	<0.001	0.23
	H/A/S	6	3.67	0.004	0.05
	R	48			0.10

Abbreviations: A, archipelago; H, habitats; R, residuals; S, sites.

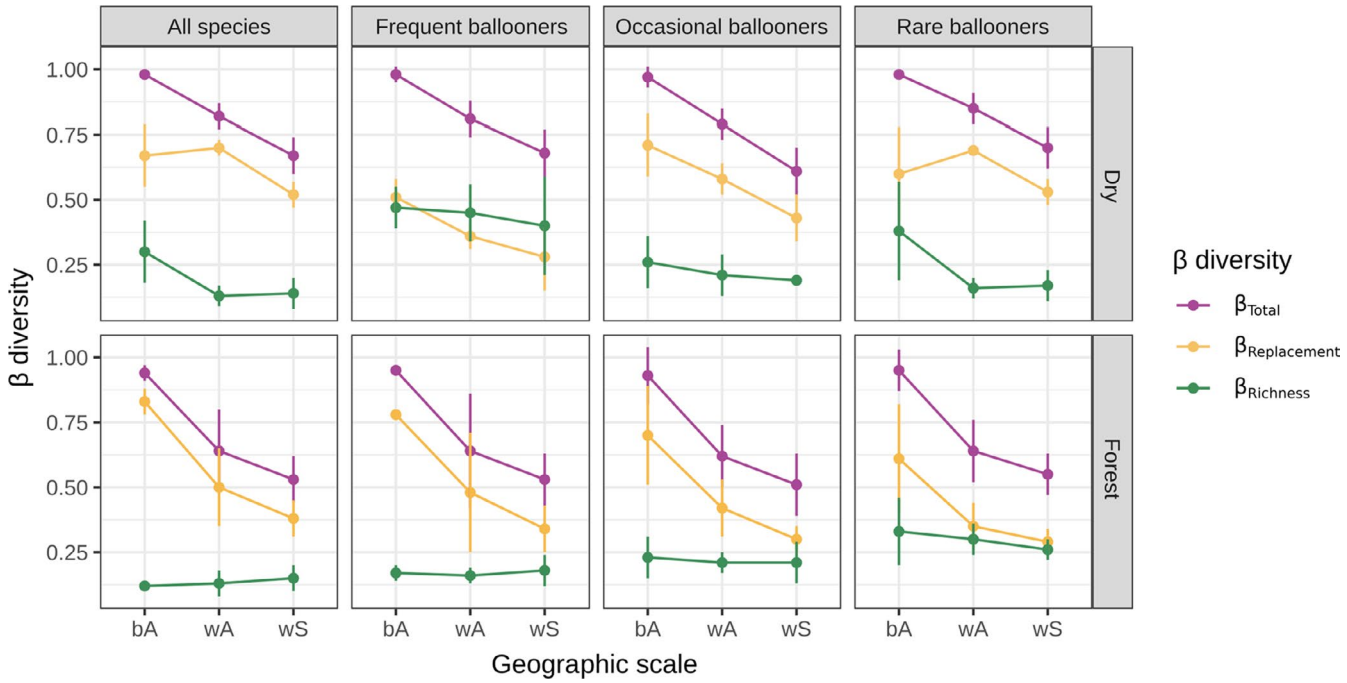

FIGURE 3 Mean β diversity (β_{Total}, $\beta_{Replacement}$ and $\beta_{Richness}$) at three geographic scales—between archipelagos (bA), between sites within archipelago (wA) and between plots within site (wS). Values correspond to analyses applied to dry habitat and forest plots and to each ballooning category separately

for frequent ballooners in dry habitats and for rare ballooners in forested areas (Figure 3).

The PerMANOVA revealed marked differences in composition between island assemblages (Table 2) and contrasting patterns in dry and forest sites. In dry sites, when all species were considered, variation in $\beta_{replacement}$ was substantially explained by the variable of islands nested in archipelagos (R^2 = 0.297) and, to a lesser extent, by archipelago (R^2 = 0.171), while $\beta_{richness}$ was highly explained by archipelago (R^2 = 0.686). Also, in dry sites, rare ballooners showed similar patterns. In contrast, in forest sites, variation in $\beta_{richness}$ was neither explained by archipelago nor islands within archipelagos (R^2 ~0), while variation in $\beta_{replacement}$ was highly explained by archipelago (R^2 = 0.616). Similar patterns were also reported for frequent ballooners and occasional ballooners.

3.3 | Community variation within habitats

According to the PERMDISP analysis, distance to the centroid within sites for $\beta_{replacement}$ was greater in dry habitats than in forests ($F_{1,49}$ = 6.57, p = 0.014, Figure 4a) when considering all species. As for the results for each ballooning category, there were no differences between habitats for frequent ballooners ($F_{1,49}$ = 0.034, p = 0.854, Figure 4b), marginal differences for occasional ballooners

TABLE 2 Results of the nested permutational multivariate analyses of variance for β diversity (β_{Total}, $\beta_{Replacement}$ and $\beta_{Richness}$) across spatial scales, for dry habitat and forest plots and for each ballooning category separately. Results include degrees of freedom (df), the *F*-ratio (*F*), the explained variance (R^2) and the *p*-values (*p*)

				All species			Frequent ballooners			Occasional ballooners			Rare ballooners		
Habitats	β diversity	Effects	df	*F*	R^2	*p*	*F*	R^2	*p*	*F*	R^2	*p*	*F*	R^2	*p*
Dry	β_{Total}	A	2	9.388	0.355	<0.001	8.407	0.347	<0.001	11.597	0.394	<0.001	7.566	0.313	<0.001
		A/S	3	3.358	0.191	<0.001	2.567	0.159	<0.001	3.903	0.199	<0.001	3.081	0.191	<0.001
		R	24		0.454			0.495			0.407			0.496	
	$\beta_{Replacement}$	A	2	3.845	0.171	<0.001	15.520	0.459	<0.001	12.832	0.405	<0.001	0.557	0.030	0.848
		A/S	3	4.468	0.297	0.001	4.197	0.186	<0.001	4.551	0.216	<0.001	4.086	0.328	<0.001
		R	24		0.532			0.355			0.379			0.642	
	$\beta_{Richness}$	A	2	26.637	0.686	<0.001	2.601	0.153	0.024	9.791	0.373	<0.001	30.950	0.706	<0.001
		A/S	3	0.123	0.005	0.995	1.577	0.139	0.114	2.959	0.169	0.026	0.584	0.020	0.669
		R	24		0.309			0.707			0.457			0.274	
Forest	β_{Total}	A	2	19.304	0.531	<0.001	18.951	0.519	<0.001	19.323	0.535	<0.001	17.542	0.521	<0.001
		A/S	3	3.347	0.138	<0.001	3.704	0.152	<0.001	3.215	0.133	0.002	2.744	0.122	<0.001
		R	24		0.330			0.329			0.332			0.357	
	$\beta_{Replacement}$	A	2	30.697	0.616	<0.001	29.807	0.589	<0.001	33.038	0.626	<0.001	28.589	0.635	<0.001
		A/S	3	4.765	0.143	<0.001	5.864	0.174	<0.001	5.177	0.147	0.002	2.940	0.098	0.024
		R	24		0.241			0.237			0.227			0.267	
	$\beta_{Richness}$	A	2	−2.537	−0.243	1.000	−0.030	−0.003	0.908	2.367	0.150	0.126	6.663	0.304	0.002
		A/S	3	0.648	0.093	0.597	0.011	0.001	0.967	0.951	0.090	0.454	2.164	0.148	0.085
		R	24		1.150			1.001			0.760			0.548	

Abbreviations: A, archipelago; A/S, sites within archipelago; R, residuals (within sites).

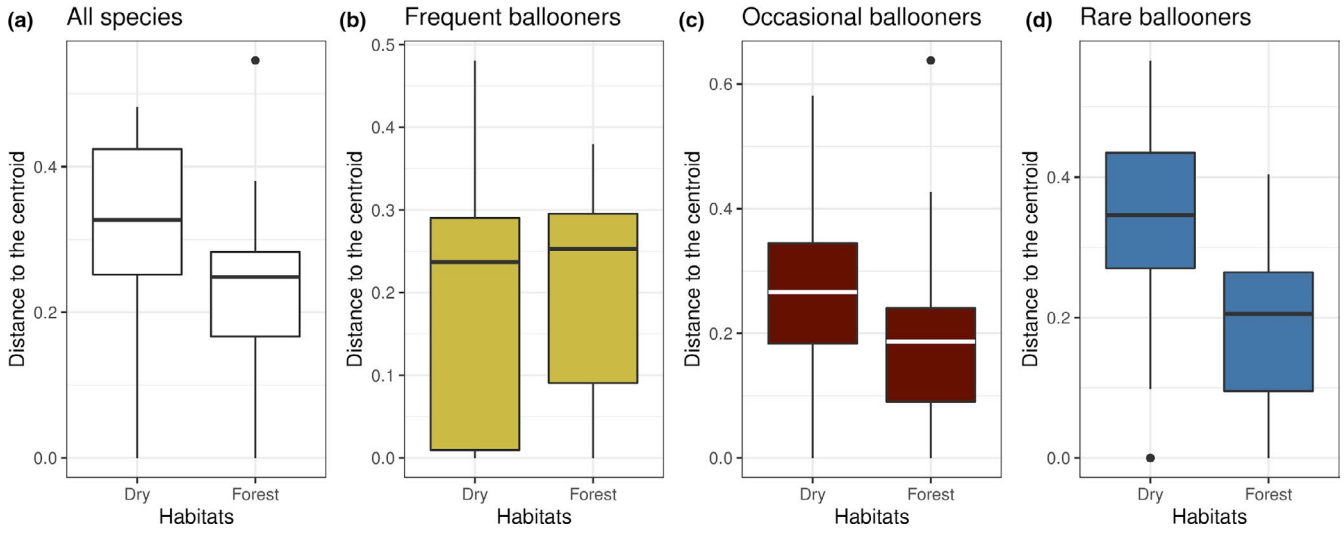

FIGURE 4 Distances of $\beta_{Replacement}$ of each plot to the centroid of its corresponding site for dry and forest habitats, for all species (a) and for each ballooning category (b–d)

($F_{1,49}$ = 4.134, p = 0.047 Figure 4c) and strong differences for rare ballooners ($F_{1,49}$ = 15.732, p < 0.001 Figure 4d). There was no clear and general pattern in the distances of the three beta components for each plot to the centroid of their respective sites across all archipelagos (Figure S1 in Appendix S3). Interestingly though, $\beta_{replacement}$ appeared to be lower in forests than in dry habitats for rare ballooners.

3.4 | Species rarity

The gambin models built from observed abundances pointed at distinct distributions in spider species abundances (SAD) between dry and forest sites, similar to log-series and to log-normal distributions respectively (Figure 5a), although differences in alpha gambin

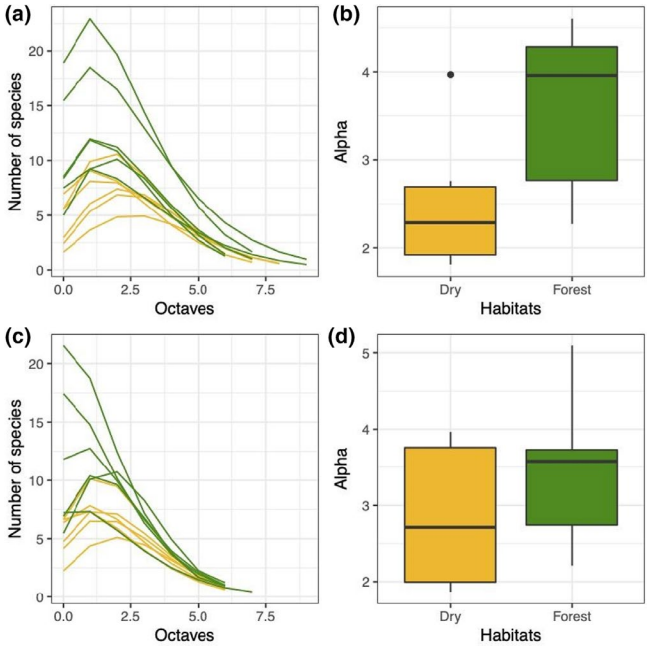

FIGURE 5 Fitted curves (a, c) and values of alpha parameter (b, d) of the gambin model for species abundance distributions of the 12 study sites. Distributions are grouped according to habitat type and whether they were standardised (c, d) or not per sample size (a, b)

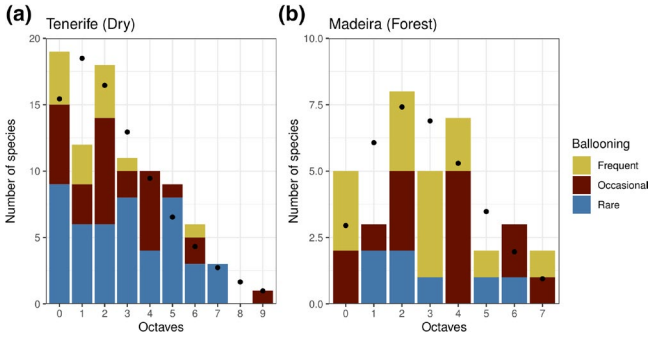

FIGURE 6 Species abundance distributions and corresponding gambin models. The dry site of the island of Tenerife (a, $\alpha = 1.811$) and forest site 2 of the island of Madeira (b, $\alpha = 4.173$) are examples of the expected and found log-series and log-normal distributions, respectively. The gambin model (black circles) is fitted to the data binned into octaves, for each of which the contribution of frequent, occasional and rare ballooners is indicated by the colour code

were marginally non-significant between habitats (Wilcoxon test $p = 0.09$, Figure 5b). When standardised, SADs were more similar between habitats (Figure 5c) and we did not find any significant differences in the standardised values of the alpha parameter between dry and forest sites (Wilcoxon test $p = 0.47$, Figure 5d). However, in dry habitats rare ballooners were on average more represented by rare species (the average of the mean weighted octave was 2.4) than occasional and frequent ballooners (2.48 and 2.55 respectively Figure 6a; Figure S2 in Appendix S3) but there were no statistical differences (Kruskal–Wallis, $p = 0.652$). Trends were similar in the forest, with averages of the mean weighted octave of 2.44, 3.59 and 2.91 for rare, occasional and frequent ballooners respectively (Figure 6b; Figure S3 in Appendix S3) but unlike in dry habitat, there were marginal significant differences between categories (Kruskal–Wallis, $p = 0.041$), with rare ballooners being different from occasional ones (post-hoc Dunn test $p = 0.006$).

4 | DISCUSSION

Here we contribute to filling in one of the major knowledge gaps in island biogeography that is the identification of within-island drivers of community diversity and structure (Patiño et al., 2017; Santos et al., 2016). More specifically, through this first standardised comparison of arthropod assemblages across Macaronesian archipelagos, not only do we support the relevance of geography and dispersal ability for the assembly of island assemblages but we also demonstrate how these effects vary depending on habitat type.

4.1 | Beta diversity and dispersal-related assemblage composition

The across-archipelago patterns in assemblage similarity that we found can be explained by the current knowledge on the ecology and biogeography of Macaronesian species. One of the first patterns that stood out was that Azorean assemblages formed a well-separated group, reflecting the greater filtering (dispersal and environmental) acting on this geographically isolated archipelago (Triantis et al., 2012). On the other end are Canarian and Madeiran forest assemblages, which were similar probably because of ongoing species exchange due to their proximity as well as their common colonising source (Iberian Peninsula; Hutsemékers et al., 2011). As for the dry habitats, the separation of the Canary Island and Madeiran assemblages may be the result of dispersal filtering—the distance to the source species pools (the Mediterranean basin) is shorter for the Canary Islands. The large differences between the assemblages of Cabo Verde and the rest of the islands/archipelagos were probably due to their remoteness and the very different origin of several terrestrial lineages, which show stronger affinities with those of adjoining sub-Saharan regions (Romeiras et al., 2019). As a result, and unlike the other Macaronesian archipelagos, there is no native forest in Cabo Verde (and all the evidence suggests that there never was), being *Dracaena draco* s.l., the only native tree common to all Macaronesian archipelagos. It must be highlighted that the so-called 'laurel' forests found in the Azores, Madeira, and the Canary Islands are absent in Cabo Verde, where some Afrotropical native trees (e.g. *Ficus sycomorus* and *Faidherbia albida*) occur (Neto et al., 2020). Therefore, our results support the view that Cabo Verde assemblages differs significantly in structure and biogeography from assemblages in the other archipelagos, and that the term "Macaronesia" should be used in a geographical sense and not to define a biogeographical unit (see for details Freitas et al., 2019).

As for the dispersal ability of species, the effects of geographic isolation and habitat type become evident. Azorean assemblages

contained a greater proportion of frequent ballooners and the smallest proportion of rare ballooners (followed by Madeiran and Canarian assemblages), which aligns with the idea that only good dispersers reach the most remote islands, while archipelagos closer to the mainland are also colonised by poor dispersers. Two potential explanations may be behind the fact that rare ballooners were more dominant and widespread in dry habitat areas than in forest areas. First, the greater structural complexity of forests is expected to lead to greater numbers of frequent ballooning species since these include more web builders. And second, frequent ballooners may be filtered out from certain types of insular open habitats as they may be too exposed to strong winds and end up at sea. In the specific case of the Azorean forest assemblages, species of the three ballooning categories were similarly widespread, probably because of the homogeneous habitat and ecological features of the Azorean forests (Triantis et al., 2012).

4.2 | Community variation across geographic scales

As expected, β diversity values were the greatest at the largest geographic scale (archipelago), which can be due to the large distances between the Macaronesian archipelagos and the differences in colonisation source, habitat and climatic conditions between them (Carvalho & Cardoso, 2014). Although the change in β diversity with geographic scale was not greater in dry habitats than in forests—contrary to what we hypothesised—in general, the trends were different and the values greater across metrics and inferred ballooning categories. Among them is the trend of $\beta_{\text{replacement}}$ among the rare ballooners of dry habitats, which show greater values between islands of the same archipelago (Figure 5). This pattern may be the result of two facts/processes. First, in dry habitats, the differences in species richness between archipelagos—the Canary Islands had far more species than Cabo Verde—is far greater than the differences in species richness between the islands of the same archipelago. And second, the very high $\beta_{\text{replacement}}$ of rarely ballooning species at the between-site (within archipelago) scale, caused by their limited dispersal ability and, perhaps, by the fact that, as a consequence of a selection process, rare ballooners from insular open habitats may tend to avoid anemochory more than their forest counterparts to prevent landing on the sea.

Overall, changes in species replacement and richness appeared to be less predictable, and more complex and variable in dry habitats than in forests. Although the patterns that we detected may be idiosyncratic to our model system, they may also reflect the greater inherent instability and variability of (insular) open habitat assemblages (Lin et al., 2020), more exposed to climatic changes and, in the case of spiders, to wind-driven dispersal.

4.3 | Community heterogeneity within habitats

Although, as we hypothesised, spider assemblages in dry habitats—all species and particularly rare ballooners—were more variable than those in forests, this pattern was evident only at the local (within-site, between plots) scale. This pattern may be explained by the fact that areas with dry habitats are more heterogeneous than forests, which leads to larger differences between local assemblages in the former (Barton et al., 2010; Zhang et al., 2018). Indeed, (micro) climatic conditions are more stable in forests—canopy or high vegetation can stabilise and homogenise humidity and temperature, creating similar microhabitat conditions and allowing the spider species adapted to those conditions to use the same resources present across larger areas (under similar conditions).

If this link between habitat and community/assemblage homogeneities on islands is confirmed, its implications for island biogeography may be significant—the 'partitioning' of the different habitat-assemblages of islands will provide novel functional and context-specific insights into the processes of community assembly. Furthermore, the ecological conclusions will be relevant for conservation strategies and policies because they will allow greater consideration of previously neglected habitats, facilitate prioritisation among them and assist deciding the size of and allowed activities in protected areas.

4.4 | Species rarity

Although not supported statistically, we found a trend of a greater rarity in dry habitat than in forest assemblages both locally (plot scale) and regionally (site scale) that matched our third hypothesis. The parameter (alpha gambin) that we used to represent or summarise SAD patterns is a powerful tool in many comparative analyses of assemblages (e.g. Matthews et al., 2014). However, this simplification into one value and the fact that our assemblages may have been too few may have led to our results. Therefore, the question remains of whether greater replication at both plot (more plots of both habitats within each island) and island levels (more islands with plots of both habitats) would lead to different findings.

One of our unexpected and most interesting findings was that poor dispersers were more prone to be rare than other species in dry habitats. It is possible that these habitats have more spatially rare microhabitats (conditions, niches) than forests and, as a consequence, contain more rare species (Calatayud et al., 2020), an idea supported by the finding that within-site dispersion levels of beta were greater in dry habitat. Furthermore, stronger environmental filtering caused by greater (micro) climatic instability in dry habitats not only may cause greater levels of rarity but also smaller species populations with greater local extinction rates (that may not be compensated by a frequent influx of migrants in the case of rare ballooners), which may ultimately lead to greater species turnover.

5 | CONCLUSIONS

Our sampling design allowed to compare trends among assemblages across multiple spatial scales, and although it also limited the number

of comparisons that could be done at the smallest (local) scale, most of our findings were clear and supported our hypotheses.

Inferred ballooning frequency appears to provide very useful information about the role of dispersal in the shaping and differentiation of dry habitat spider assemblages, even when the species are classified mainly by family. As species or population-specific ballooning data become available, we might discover more specific trends (e.g. differences between native and introduced species caused by reduced ballooning frequency among the former) and their effects on spider species assembly on islands. Our findings reveal that the type (and perhaps structure) of habitat does not only condition the processes behind insular community assembly but also the scale at which they occur. Future studies should not only compare differences between assemblages within other habitat types, but should also look at the causes and drivers behind them, for example, the role of habitat structure and heterogeneity on spider assemblages at the local scale, particularly in dry habitats. Nevertheless, our findings are highly relevant for theories on across and within island community assembly as well as for biodiversity conservation.

Forests are usually considered as home and cradles of extraordinary levels of biodiversity, and, undoubtedly, much effort should be placed on conserving them. However, dry, open (and often modified) habitats should not be neglected because, as in the case of Macaronesian islands, can contain unexpected levels of (local) spatial variability and uniqueness, and therefore, can be of much conservation value and excellent model systems to test new ecological theories.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest regarding this publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on Dryad (https://doi.org/10.5061/dryad.t4b8gtj2t).

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BIOSKETCH

Jagoba Malumbres-Olarte is an ecologist interested in the eco-evolutionary processes behind the formation of biodiversity (particularly arthropods) and in developing scientific and educational tools for its conservation. The research of our groups focuses on island biology—the biogeographic and ecological processes behind the shaping of species communities. J.M.-O., F.R., P.C. and P.A.V.B. conceived the ideas; all authors contribute to generating the data; J.M.-O. and F.R. analysed the data; and J.M.-O., F.R., P.C. and P.A.V.B. led the writing.

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SUPPORTING INFORMATION

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